

Magnitude of seasonal variation in population abundances of the agile frog *Rana dalmatina*

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During recent decades, amphibians have experienced population decline worldwide (e.g., Barinaga, 1990; Wake, 1991; Stuart et al., 2004). More than 41% of amphibian species are currently considered as threatened (Pimm et al., 2014). There are many reasons for these declines (review in Collins and Storfer, 2003; Semlitsch, 2003; Beebee and Griffiths, 2005), and there frequently are indirect and interrelated effects (Kiesecker and Blaustein, 1995; Kiesecker et al., 2001; Blaustein et al., 2011). Amphibian declines and disappearances have led to mounting emphasis on monitoring amphibian population abundances (e.g., Houlahan et al., 2000; Stuart et al., 2004). Typically, however, amphibian populations are characterized by great natural fluctuation (Marsh, 2001; Marsh and Trenham, 2001), and it is challenging to separate human impacts from such fluctuation (Pechmann et al., 1991; Pechmann and Wilbur, 1994; Green, 2003; Pechmann, 2003).

It has been found that the magnitude of population fluctuation may indicate the risk of local extinction from demographic or environmental stochasticity (Leigh, 1981; Goodman, 1987; Engen and Saether, 1998). Pond-breeding amphibians with biphasic life histories, and especially those frogs with high fecundity, are typical of high variance in population changes and high rates of local extinction (Green, 2003). Therefore, understanding the magnitude, trends, and causes of population variation, which is key for amphibian conservation, depends upon long-term studies on population abundances (Marsh, 2001; Collins and Halliday, 2005).

Even as monitoring of population trends for amphibians should encompass adequate time periods, it is also important that this monitoring cover sufficiently large areas. Studies of one or several local populations, whatever their length, do not necessarily represent the situation prevailing in the population as a whole. Therefore, a group of local populations representing the entire population is more appropriate for assessing population trends in amphibians (Lawton, 2000). Most long data series, however, have focused only on single locations (e.g., Pechmann et al., 1991; Semlitsch et al., 1996; Todd et al., 2010). On the other hand, among

studies assessing trends at regional (e.g., Hecnar and M'Closkey, 1996; Lecis and Norris, 2004) or global (Houlahan et al., 2000; Stuart et al., 2004) scales, short data series predominate. There is thus a dearth of long-term studies at overall population level (but see Meyer et al., 1998; Loman and Andersson, 2007), because this monitoring is quite expensive and time-consuming. Therefore, the conservation potential of any such study is enormous.

We present here results from 11 years (2005–2015) of monitoring abundances of agile frog (*Rana dalmatina*) clutches conducted at 134 ponds on the Hornojiřetínská spoil bank in the North Bohemian Brown Coal Basin in the Czech Republic. *R. dalmatina* is a representative of European pond-breeding frogs and it forms a large population consisting of many local populations (breeding ponds) on the studied spoil bank. Such a population constitutes a unique environment for answering the following questions related to amphibian fluctuations: (1) How much fluctuation is possible for *R. dalmatina* abundance and in the numbers of ponds with frog clutches? (2) Do decreases in clutch numbers between two consecutive years outnumber increases, as can be expected from surveying the literature (Alford and Richards, 1999), and particularly in the case of pond-breeding amphibians (Green, 2003)? (3) Are clutch numbers and the numbers of occupied ponds correlated? In other words, is it possible to use the number of local populations – in this study occupied ponds (breeding sites) – as a more easily ascertained population parameter in place of the entire population size for quantifying long-term trends in large amphibian populations?

1 Materials and Methods

1.1 Study area

The Hornojiřetínská spoil bank (50°35′N, 13°35′E) is situated in the North Bohemian Brown Coal Basin (Fig. 1). Covering an area of about 7 km², it is one of the largest spoil

banks in the Czech Republic. About one-half of the spoil bank (351.28 ha) has been technically reclaimed. Within this part, primarily heterogeneous terrain was planned, and, instead of leaving hundreds of ponds in terrain depressions, only eight larger waterbodies were left or newly created. In the second half of the spoil bank, which is technically unreclaimed, on the other hand, more than 300 waterbodies have been identified on an area of 352.71 ha (Doležalová et al., 2012).

Due to the partial absence of technical reclamation and the spoil bank's considerable age (about 40–50 years after heaping), the vegetation cover is diverse, consisting mainly of herb vegetation with scattered shrubs, trees, and light forests (Prach, 1987; Prach et al., 1999). In addition to a considerable number of reproductive habitats, the spoil bank therefore also provides amphibians with a suitable terrestrial environment (Doležalová et al., 2012). Eight species of amphibians, including a large *R. dalmatina* population with more than 140 breeding sites, have been recorded on the spoil bank (Smolová et al., 2010).

1.2 Study species and estimation of its abundance

The studied species, *R. dalmatina*, is a European pond-breeding ranid frog occurring in the southern and central parts of the continent (Arnold and Ovenden, 2004). The species breeds in still waterbodies, often in or close to woodlands (usually light deciduous forests) where the frogs live during other parts of the year (Gasc et al., 2004). The Czech Republic includes the northern limit of this species' continuous range in Europe (Rehák, 1992). In this country, it occurs mainly in warmer regions and at lower elevations up to 400–600 m a.s.l., where it inhabits bright broadleaf forests, alluvial forests, forest steppes and xerothermic grass stands (Moravec, 1994). *R. dalmatina* is not very discriminating in its selection of reproductive habitat. It reproduces in waterbodies of various types having aquatic vegetation (Rehák, 1992; Kuzmin, 1999).

Inasmuch as this is a temperate pond-breeding frog with relatively high fecundity (Solský et al., 2014), we could expect in this species great variance in population abundance and thus a high rate of local extinction from demographic and environmental stochasticity (Green, 2003). *R. dalmatina* is therefore a very suitable species for studying population dynamics. In contrast to many other amphibian species, moreover, this species' population size can be rather easily and accurately determined based upon counting its clutches. Clutches are placed in those parts of waterbodies overgrown with vegetation (Ficetola et al., 2006; Hartel, 2008; Dodd, 2010). Due to male breeding territoriality, each pair lays a well-separated and easily distinguishable egg clutch (Schneider, 1996; Lesbarrères and Lodé, 2002; Hartel et al., 2009). *R. dalmatina* females produce only a single clutch per breeding season (Rehák, 1992; Lodé et al., 2005). Furthermore, because the species spawns early in the season, when low temperatures inhibit egg development, there is sufficient time to count clutches and examine clutch sizes before they hatch (Bernini et al., 2004). Therefore, the number of clutches frequently has been used in estimating population abundance for this species (e.g., Crouch and Paton, 2000; Loman, 2002; Hartel, 2005; Ficetola et al., 2006).

R. dalmatina abundance was determined within the Hornojiřetínská spoil bank for 11 consecutive years, from 2005 to 2015. In the first year of monitoring, we found 182 ponds. In subsequent years, previously discovered sites were relocated based on the position recorded using manual GPS devices (various equipment sold by Garmin). Meanwhile, new locations were found each year as part of systematically exploring the spoil bank. The number of monitored waterbodies therefore increased over the course of monitoring. The study area contained 333 ponds, of which 134 were monitored each year for the entire studied period and included into the study. We detected and counted *R. dalmatina* clutches by slowly walking at a constant speed through littoral vegetation in pond areas with maximum depths of nearly

1.3 m, as these parts are well-suited for clutch laying by this species (Rehák, 1992). We always counted after the main phase of clutch laying (usually in the first half of April).

1.3 Statistical analysis

We used Pearson's chi-squared test to compare whether overall clutch numbers at the 134 permanently monitored ponds differed among years. We used the same method to compare numbers of ponds with *R. dalmatina* clutches (i.e., pond occupancy). Using simple linear regression, we examined the existence of linear trends in both clutch numbers and pond occupancy (dependent variables) during the studied period (independent variable). We tested the hypothesis of correlation between clutch numbers and pond occupancy using Pearson's product-moment correlation.

We assessed population changes between two consecutive years as the ratio of clutch number at time t+1 divided by clutch number at time t (n_{t+1}/n_t). Decreases therefore resulted in values of <1 while increases resulted in values of >1. Mean decrease and mean increase in clutch number among years were compared using the nonparametric Mann–Whitney U test. Variance between absolute values of decreases and increases was compared using the nonparametric Fligner–Killeen test. To express and compare the ranges of decreases and increases, we used the higher clutch number divided by the lower clutch number between two consecutive years (regardless of the chronological order of the years). Had we used only the ratio of values according to the above equation (n_{t+1}/n_t), we would not have been able to compare the ranges of decreases and increases inasmuch as decreases would result in values between 0 and 1 while increases would theoretically have no limit and could assume values between 1 and infinity. All analyses were carried out in R (R Development Core Team, 2013).

2 Results

During the 11 years of monitoring *R. dalmatina* clutches at 134 ponds, we found a total of 8,410 clutches. Annual clutch numbers demonstrated significant year-to-year differences ($\chi^2 = 2,965.69$, df = 10, $p < 10^{-6}$) and fluctuated more than tenfold (10.34×) within the studied period (mean ± SD: 765 ± 417 clutches, min. = 155, max. = 1,603), but the data showed no linear trends (F = 1.47, df = 1, p = 0.26; Fig. 2). In addition, the numbers of ponds with frog clutches varied greatly among years ($\chi^2 = 47.68$, df = 10, $p < 10^{-6}$; Table 1), albeit without any linear trends (F = 0.22, df = 1, p = 0.65; Fig. 2). The total clutch numbers did, however, correlate highly positively with the numbers of colonized ponds (r = 0.80, 95% CI for r = 0.39–0.95, t = 4.06, df = 9, p = 0.003).

Decreases slightly outnumbered increases (6 vs. 4 of the total 10 population changes between years), exhibited a greater range than did increases (1.07–6.40 vs. 1.69–2.41), and occurred in a longer consecutive period (max. 5 years vs. 2 years). A more detailed analysis of year-to-year changes, however, revealed that within the 6 decreases only 2 were more substantial (decreases in clutch number to 48% and 16% of the clutch number from the previous year) and for none of the 4 slight decreases did the number of clutches fall to below 80% of the value from the previous year (Table 1). The mean increase in clutch number (mean \pm SD: 420 \pm 306 clutches) was slightly greater than was the mean decrease (313 \pm 329), although this difference was not significant (W = 9, p = 0.61), probably reflecting the small sample size (comparing the means of 4 and 6 values) and thus low power of the test (Crawley, 2007). Given that decreases (1,878 clutches) was greater than was the total of increases (1,679). Similarly, there were no significant differences in variance between absolute values of decreases and increases ($\chi^2 = 1.61$, df = 1, p = 0.21).

3 Discussion

3.1 Magnitude of variation in R. dalmatina population abundances

Collins and Halliday (2005) had concluded that adult population size in amphibians may vary by some 20 times over just a few years' time and that only long-term studies are able to identify meaningful population trends amidst inter-annual variability in population size. Within our 11-year study, annual clutch numbers of *R. dalmatina* fluctuated more than 10-fold. Although there have been a number of studies on amphibian population dynamics (e.g., Marsh, 2001; Green, 2003) and there is almost universal agreement as to the existence of natural fluctuation in amphibian population size (Alford and Richards, 1999), studies describing the magnitude of natural fluctuation in amphibians are scarce (reviewed, e.g., in Pechmann and Wilbur, 1994).

Although number of studies have examined amphibian population size, they have been focused on aspects other than describing the range of fluctuation. By comparing the magnitude of population fluctuation within long-term studies (those longer than 10 years) on Central European pond-breeding ranid frogs, genus *Rana (R. temporaria, R. dalmatina* and *R. arvalis)*, we determined that: (i) the size of all seven monitored populations was determined based on clutch numbers; (ii) annual clutch numbers of *Rana* species have been observed to fluctuate between 2.49-fold in *R. dalmatina* (Bancila et al., 2015) and 10.34-fold in the same species (this study); (iii) mean fluctuation in those species monitored was 6.2-fold with very small differences among species (*R. temporaria* – 5.49-fold, *R. dalmatina* – 6.42-fold, and *R. arvalis* – 6.35-fold); (iv) the ranges of fluctuation determined did not increase with monitoring duration, which finding is in conflict with generally accepted assumptions (Pechmann and Wilbur, 1994) (Table 2); (v) clutch numbers varied significantly within the studies among years; and (vi) most of the studies (excluding those dedicated to *R. dalmatina*, i.e., this study and Bancila et al., 2015) displayed significant linear trends (Table 3).

3.2 Ratio of population decreases to increases

In our study, decreases slightly outnumbered increases (60% vs. 40% of inter-annual changes). According to the assumptions of Alford and Richards (1999), longer periods of continual decrease are interrupted by occasional events of high recruitment in amphibians, and the prevalence of population decreases therefore does not necessarily mean that a population is in decline. Similar conclusions had been reached also by Meyer et al. (1998). In the meta-analysis of Green (2003), conducted across 89 species, 617 time-series, and 4,482 census intervals, declines (50.6%) outnumbered increases (45.1%). Within amphibians grouped according to their life-history characteristics, population declines were the most dominant among pond-breeding frogs (51.1% vs. 44.8%) while this ratio was much more balanced within other amphibian groups (max. difference of 1.4%). In contrast, Hartel (2005) recorded more year-on-year increases than decreases.

Similarly conflicting results were determined also within our own comparison of studies of three ranid frogs species (Table 2). Within seven assessed populations, three populations had mostly decreases, three had mostly increases, and one had a balanced ratio of year-on-year decreases and increases. The ratios of decreases and increases in abundance were, however, relatively balanced within these populations and ranged from 60% vs. 40% to 36% vs. 64% (decreases vs. increases), with an overall balanced ratio of decreases to increases (49% vs. 51%).

Concerning the range of year-on-year decreases and increases, it can be expected based on the assumptions of Alford and Richards (1999) that year-on-year increases in abundance should be much greater (and last for less time) than should population decreases due to the aforementioned occasional events of high recruitment. Our results only partially agreed with this assumption, as even though year-on-year decreases lasted for longer continuous periods, they demonstrated a greater range than did increases (Table 2). Within the seven assessed

populations of ranid frogs, population increases had wider ranges than did decreases in five populations, although the differences were not very large. For the two remaining populations, in contrast, the ranges of decreases were rather substantially wider than were those of population increases (Table 2).

3.3 Comparison of clutch numbers and numbers of occupied ponds

As true of clutch numbers, the numbers of ponds with frog clutches varied greatly among years and manifested no linear trends during this time. Finally, numbers of clutches and of occupied ponds were highly positively correlated. As both monitored parameters (i.e., clutch numbers and numbers of occupied ponds) behave very similarly over the long term (Fig. 2) and are highly correlated, it can be assumed that they are interchangeable. This phenomenon is useful especially where there are large amphibian populations consisting of many local populations. In such populations, monitoring the entire population size would be very demanding of both time and money. Monitoring population size can therefore be replaced by the easier and less costly alternative of monitoring the number of occupied ponds, which may be a simplified representation of local populations. As a number of amphibian species actually create such a complex of local populations (e.g. Alford and Richards, 1999), this approach could be applied to quantifying long-term trends in many amphibian populations, or rather its application could be used to increase the proportion of populations that could be monitored.

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Year	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	Mean
Abundance	830	400	729	1603	1296	1150	1075	168	155	373	631	765
Pond occupancy (%)	52 (38.5)	46 (34.1)	64 (47.4)	66 (48.9)	69 (51.1)	84 (62.2)	85 (63.4)	38 (28.1)	38 (28.1)	44 (32.6)	60 (44.7)	59 (43.5)

Study	Species	Period	Nyears	Range	Mean	F _{times}	SD	CV	N _{dec}	N _{inc}	Range _{dec}	Range _{inc}
This study	RaDa	2005–2015	11	155–1,603	765	10.34	417	0.55	6 (60%)	4 (40%)	1.07-6.40	1.69–2.41
Bancila et al. 2015	RaDa	1997–2011	15	233–581	393	2.49	112.54	0.29	7 (50%)	7 (50%)	1.02-2.00	1.05-2.30
Hartel and Moga 2007	RaTe	1997–2007	11	8–65	26	8.13	16.73	0.64	6 (60%)	4 (40%)	1.05-3.25	1.16-1.60
Loman and Anderson 2007	RaTe	1989–2005	17	357-1,500	800	4.20	320.41	0.40	6 (38%)	10 (62%)	1.24–1.82	1.01-2.00
	RaAr	1989–2005	17	150–1,450	754	9.67	372.42	0.49	7 (44%)	9 (56%)	1.15-2.17	1.15-2.58
Lyapkov et al. 2006	RaTe	1982–1993	12	2,667–11,067	5,211	4.15	2,841.72	0.55	4 (36%)	7 (64%)	1.22-2.27	1.06-2.44
	RaAr	1982–1993	12	4,667–14,133	8,450	3.03	2,828.05	0.33	6 (55%)	5 (45%)	1.06–1.79	1.03-2.13

12 4,667–14,133 8,450

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Study	Species	Clutch	ers	Linear trends				
	Species	χ ²	df	р	F	df	р	Trend
This study	RaDa	2,965.69	10	< 10 ⁻⁶	1.47	9	0.26	\leftrightarrow
Bancila et al. 2015	RaDa	450.89	14	< 10 ⁻⁶	1.32	13	0.27	\leftrightarrow
Hartel and Moga 2007	RaTe	88.61	10	< 10 ⁻⁶	9.86	9	0.01	\downarrow
oman and Anderson 2007	RaTe	2,052.58	16	< 10 ⁻⁶	9.04	15	0.009	1
	RaAr	2,933.95	16	< 10 ⁻⁶	14.79	15	0.002	\downarrow
Lyapkov et al. 2006	RaTe	17,045.6	11	< 10 ⁻⁶	6.46	10	0.03	1
	RaAr	10,411.42	11	< 10 ⁻⁶	6.19	10	0.03	↓

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Fig 1 Study area. Hornojiřetínská spoil bank situated in the North Bohemian Brown Coal Basin in the Czech Republic 199x200mm (300 x 300 DPI) Year

78x38mm (300 x 300 DPI)

Abundance

Occupancy



